XXVI. *On the Formation and Use of the Air-sacs and Dilated Tracheæ in Insects.* *By* George Newport, *Esq.*, *F.R.S.*, *F.L.S.* *&c.* *&c.*

Read December 7th, 1847.

It is well known to every comparative anatomist, who has paid any attention to the *Invertebrata*, that many insects in their perfect state have their respiratory organs more or less dilated, in different parts of their course, into vesicles, or sacs. In some tribes, as in most of the *Hymenoptera*, *Lepidoptera* and *Diptera*, these sacs are present in almost every species, and occupy a large portion of the interior of the body, more especially of the abdominal region. In the most active *Neuroptera* the sacs are very numerous and capacious, especially in the *Dragon-flies*; but they are much smaller and fewer in number in the *Ephemeræ*, the *Sialidæ* and the *Scorpion-flies*. In the *Coleoptera* the sacs exist only in the volant species, and are more or less numerous and capacious in these in proportion to the bulkiness of the insect, and its degree of activity on the wing. This difference exists not only in different genera, but in different species of the same genus, according as they are winged or apterous species. Thus distinct vesicles are found in the winged *Carabidæ*, but not in the apterous, in which the respiratory organs are simply tracheal. In the more heavy-bodied genera the vesicles are not confined to the abdominal and thoracic regions, but are sometimes extended into other parts, as in the unwieldy *Stag-beetles*, in which they are extremely numerous, and occupy the chief portion of the interior of the mandibles. In the *Lepidoptera*, as in the *Neuroptera*, they are largest in the swiftest and most powerful species, and more especially so in those in the males, which are known to be the most active on the wing. On the contrary, in the majority of the *Orthoptera*, which are merely saltatorial in their habits, the tracheæ never assume the form of distinct vesicles, excepting in a few genera, which have the power of flight. They retain the arborescent form in the perfect as in the larva state, but are

considerably enlarged throughout the greater part of their course, their extreme ramifications only retaining their original setiform structure and distribution. In the truly apterous insects the tracheæ are invariably arborescent, and diminish in size from their origin to their extremest point in their perfect as in their larva condition; and they are invariably smaller in diameter, and have fewer ramifications, in the most inactive species.

The respiratory organs are always simply tracheal in the larva state of all insects, and it is not until the period of change to the pupa is fast approaching that they begin to be enlarged, even in those in which vesicles afterwards are most numerous. The enlargement, as I have elsewhere shown*, commences in Lepidopterous insects at about the time when the larva ceases to feed. It is perceptible first in the longitudinal tracheæ of the thoracic segments of the Sphinx, immediately before the insect enters the earth; and by the time that the cell in which it is to undergo its transformation is completed, the tracheæ from the second to the fifth spiracles are distinctly enlarged. In the Diurnal species, which do not enter the earth, but undergo their changes in the open air, the dilatation of these tracheæ commences while the insects are spinning their silken threads. When this labour is finished, and they have remained for a few hours at rest, the skin is fissured along the dorsal surface of the thoracic segments and thrown off, the change to the pupa is effected, and the longitudinal tracheæ in the fifth and sixth segments are dilated into vesicles, which continue to be enlarged during the first few days after the change. The tracheæ of the third and fourth segments each give off a small trunk on their external surface, which is divided into two branches, and is involved in a fold of the new tegument that is formed beneath the old skin of the larva some days before its change. The fold of tegument on each side of the third and fourth segments is supplied with ramifications of tracheæ from these minute trunks, and very closely resembles in appearance the external abdominal branchiæ of the aquatic larvæ of *Neuroptera*. It is these folds which become the most important organs in the perfect state of the insect, its wings. When the old skin of the larva is fissured, and the thoracic segments become shortened, as the skin is thrown off, previous to their forming one region, the thorax, the trachcæ in these folds are rapidly enlarged

* Phil. Trans. 1836, part ii. p. 535.

and elongated, and mainly assist in inducing a rush of blood into these structures, which are thus expanded on the sides of the new pupa as the rudimentary wings. This elongation of the small trunks at the sides of the longitudinal tracheæ in the thorax, relieves them of a portion of that tension which results from the powerful respiratory efforts of the insect in effecting its change; and which, with a tendency to enlarge by the natural forces of growth in these structures, results in the dilatation first of the tracheæ at the base of the abdomen, and afterwards of those of the thorax, and the sides of the abdomen, into distinct sacs. This is the manner in which the air-sacs are formed in all insects. After the main trunks have become dilated their ramifications also are enlarged in like manner, and this enlargement continues from the time when the insect enters its pupa, to that of its appearance in the perfect state.

But although we are enabled to show the manner in which the vesicles are formed, it is difficult to give direct proof of their immediate use. It is assumed from the facts I have mentioned, that they are most numerous and large in volant insects, and entirely absent in apterous, that they are connected with the power of flight; but in what way, has never yet, so far as I am aware, been actually proved. It was assumed by John Hunter that they are for the purpose of enabling the insect to alter the specific gravity of its body,—a view which I have myself long ago adopted,—but the facts on which the opinion is founded are only those of anatomy, and not of direct observation or experiment, which are required to confirm it. Anatomical facts alone, as will be seen in this instance, although the safest guides, are not always sufficient. Thus we find that a vesicular structure of the organs of respiration exists in the whole of the air-breathing *Vertebrata*. The lungs of Man and the *Mammalia* are formed of multitudes of vesicles, which are more numerous than in any other class; those of *Birds* exhibit a like condition, but in these the vesicles are distributed more extensively over the whole body. A vesicular condition of the respiratory organs exists also in the *Reptiles* and *Amphibia*, but far less extensively than in *Birds*. Thus each of these classes agrees with insects in possessing a vesicular form of the respiratory organs. The whole of them also, excepting the *Mammalia*, agree in the fact that the vesicles are parietal, that the tracheal structures are dilated in different parts of their

course, while in *Mammalia* this is not the case, the vesicles in them being only at the extremities of the ramifications of the respiratory structures.

In what way then will the anatomy of the structures lead us to a well-founded inference that is supported by direct observation on the function? We must compare insects with those animals which approach nearest to them in the function of these structures,—Birds. In Birds the respiratory organs are not only vesicular, but are more extensively distributed over the whole body than in any other Vertebrata. These, as every anatomist knows, are not confined merely to the great cavities of the body, but are extended to every part of the skeleton, as in insects. They communicate directly with the interior of the bones of the wings and legs, as the tracheæ of the thorax are extended also into these parts in insects. This distribution in both is more extensive and complete in the most active species. In Birds which are unaccustomed to flight, as in the Ostrich, as remarked by Mr. Owen*, the communications of the respiratory organs with the bones is imperfect; whilst in Insects, although tracheæ exist in all, the vesicles are found only in those of flight. This fact extends even to the sexes of the same species. Thus vesicles exist in the male of the common Glow-worm, which is winged, and designed to search out the apterous female, in which the respiratory organs are simply tracheal. The like conditions exist in the common winter-moth, *Geometra brumaria*. In the male of this insect I have found the vesicles large and numerous, but not a trace of these occurs in the female. The tracheæ in this sex, which has only the rudiments of wings, are larger relatively than in the female Glow-worm, and are precisely in that condition in which I have found them in the Diurnal Lepidoptera shortly before changing to the pupa. These anatomical facts are inferential of the real use of the vesicles, and are supported by an observation which I have been able to make on the common Dung-beetle, *Geotrupes stercorarius*, at the moment when it is preparing to take flight. A specimen of this insect which had been in confinement for about twenty-four hours, and consequently had not expanded its wings during that time, when placed on a table immediately prepared to escape. After walking away quickly for a short distance it began to respire freely, alternately shortening and elongating its abdominal segments at the rate of about forty respi-

* Cyclop. of Anatomy and Physiology, art. "*Aves*," vol. i. p. 341.

rations per minute. It then ceased for an instant, and slightly separated its elytra without elevating them, and bégan again to respire more rapidly. At first its respiration was slowly but gradually increased, until a few seconds before it attempted to expand its wings and to elevate itself upon them, when the acts of respiration became exceedingly rapid, and amounted to at least 120 per minute. These were most rapidly performed, and were then suddenly arrested at the instant before it attempted to unfold the wings. During this increased respiration the abdomen of the insect was distinctly enlarged, and it was quite evident that this enlargement, and the expansion of its wings, were being effected by forced inspirations, and maintained by the expansion of the air-sacs over the whole body, and the communication of these with the tracheal vessels in the wings themselves. As however the wings had become stiffened and dried through many hours, it did not completely succeed in its attempts to escape, but only partially raised itself upon them. The results were nevertheless sufficiently satisfactory to prove to me that the respiratory organs became distended previous to the act of flight, as the entire body was distinctly enlarged; the effect of which enlargement, together with an increased evolution of heat in the body, as the result of increased respiration, must, of consequence, be to diminish the specific gravity of the insect, and thus, by lessening the degree of muscular force required to raise it on its wings, considerably augment its powers of locomotion, which seems to be the chief use for which the vesicles are developed.